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ORIGINAL
ARTICLE

Matching species traits to projected threats and opportunities from climate change

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ABSTRACT

Aim Climate change can lead to decreased climatic suitability within species' distributions, increased fragmentation of climatically suitable space, and/or emergence of newly suitable areas outside present distributions. Each of these extrinsic threats and opportunities potentially interacts with specific intrinsic traits of species, yet this specificity is seldom considered in risk assessments. We present an analytical framework for examining projections of climate change-induced threats and opportunities with reference to traits that are likely to mediate species' responses, and illustrate the applicability of the framework.

Location Sub-Saharan Africa.

Methods We applied the framework to 195 sub-Saharan African amphibians with both available bioclimatic envelope model projections for the mid-21st century and trait data. Excluded were 500 narrow-ranging species mainly from montane areas. For each of projected losses, increased fragmentation and gains of climate space, we selected potential response-mediating traits and examined the spatial overlap with vulnerability due to these traits. We examined the overlap for all species, and individually for groups of species with different combinations of threats and opportunities.

Results In the Congo Basin and arid Southern Africa, projected losses for wide-ranging amphibians were compounded by sensitivity to climatic variation, and expected gains were precluded by poor dispersal ability. The spatial overlap between exposure and vulnerability was more pronounced for species projected to have their climate space contracting *in situ* or shifting to distant geographical areas. Our results exclude the potential exposure of narrow-ranging species to shrinking climates in the African tropical mountains.

Main conclusions We illustrate the application of a framework combining spatial projections of climate change exposure with traits that are likely to mediate species' responses. Although the proposed framework carries several assumptions that require further scrutiny, its application adds a degree of realism to familiar assessments that consider all species to be equally affected by climate change-induced threats and opportunities.

Keywords

Africa, amphibian, bioclimatic envelope model, climate change exposure, dispersal, plasticity, reproductive output, trait, vulnerability.

INTRODUCTION

Fingerprints of recent climate change impacts on species' distributions are already apparent (Parmesan & Yohe, 2003), but predicting future climate change impacts is still a major

scientific challenge (Pereira *et al.*, 2010). Predictions of species' exposure to climate change have to date relied mostly on bioclimatic envelope models, and are increasingly being complemented with available trait data to estimate species' vulnerability (e.g. Heikkinen *et al.*, 2009). Assessing the risk

of species' extinction or decline requires an understanding of threats, or extrinsic adverse events, and vulnerability, or the intrinsic susceptibility of species to threats (Araújo & Williams, 2000). It is thus important to understand the interaction between threats and vulnerability, as specific traits are likely to mediate species' responses to different threats (Isaac & Cowlshaw, 2004; Fritz *et al.*, 2009; Murray *et al.*, 2011; González-Suárez *et al.*, 2013). For example, under habitat-modifying processes such as agriculture and logging, small-sized, habitat specialist mammals are most affected, whereas under processes that directly affect survival, such as hunting, the most susceptible are mammals with large body size and small litter size (González-Suárez *et al.*, 2013; see also Isaac & Cowlshaw, 2004). In climate change risk assessments, however, this specificity in the interaction between threat and vulnerability has not been addressed sufficiently.

In studies using bioclimatic envelope models, the level of species' exposure to climate change is commonly inferred from temporal changes in the overall size of species' climatically suitable space (e.g. Thuiller *et al.*, 2005b; Araújo *et al.*, 2006; Huntley *et al.*, 2006; Feeley *et al.*, 2012; Triviño *et al.*, 2013). Such summary measures conceal different opportunities as well as threats, each imposing specific constraints on species (Thomas *et al.*, 2011). First, loss of climatic suitability within existing distributions is expected to affect the persistence of local populations (e.g. Sinervo *et al.*, 2010). Second, even where suitable climate space persists, it may become more fragmented. Areas of suitable climate may lose contiguity, with fragments becoming more isolated and smaller in area. Third, gains of climatic suitability outside current distributions of species bring potential opportunities for colonization. These components of exposure are likely to have distinct spatial distributions and conservation implications, but are seldom teased apart (but see Midgley *et al.*, 2003; Heikkinen *et al.*, 2009; Araújo *et al.*, 2011).

Species also vary in their degree of intrinsic sensitivity and capacity to adapt to exposure (Williams *et al.*, 2008; Chevin *et al.*, 2010), and traits can capture this variation. Traits are meant as 'any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization' (*sensu* Violle *et al.*, 2007, p. 884). Examples are limb or wing length, and clutch size. In many cases, ecological characteristics of species and their geographical or environmental ranges are used as proxies for traits, in the expectation that they summarize combinations of traits. Examples are species' geographical range size and climatic breadth.

Previous research has identified general traits that predispose species to extinction (e.g. Purvis *et al.*, 2000), and specific traits that mediate the effect of particular threats on species (Isaac & Cowlshaw, 2004; Murray *et al.*, 2011; González-Suárez *et al.*, 2013). Under changing climates, poor dispersal ability and habitat or climatic specialization, for example, have been suggested to increase vulnerability

(Peters & Darling, 1985), and have been found to correlate positively with empirical data on range contractions (Beaumont & Hughes, 2002; Botts *et al.*, 2013). Generally, traits have accounted for a significant but small amount of the variation in climate change-induced range shifts (Buckley & Kingsolver, 2012). Yet, changes in the size, level of fragmentation and position of species' climate space each represent a distinct threat or opportunity under changing climates, and thus are likely to interact with particular sets of 'response-mediating' traits (*sensu* Luck *et al.*, 2012).

Besides evolution on longer time-scales, three main determinants of climate change vulnerability can be distinguished (Williams *et al.*, 2008; Chevin *et al.*, 2010). First, traits describing plasticity of individual phenology, behaviour or physiology affect the potential of individuals to persist *in situ* under changing climates. For example, species able to physiologically tolerate a wide range of climatic variation (Huey *et al.*, 2012), or adapt their behaviour to lessen exposure to unsuitable climates (Chown, 2012), have, all else being equal, higher chances of persistence *in situ* under climate change. Second, traits influencing the potential of individuals to disperse affect their capacity to colonize newly suitable environments (Pöyry *et al.*, 2009) or move between fragments of suitable climate. Third, life-history traits influencing population growth, although not affected by environmental change, may constrain the rate of dispersal or *in situ* adaptation. In the case of reproductive traits, for example, frequent or early reproduction and high fecundity, should increase colonization opportunities (Angert *et al.*, 2011).

Here, we present an analytical framework for examining projections of climate change-induced threats or opportunities for species with reference to the vulnerability of species. Each threat or opportunity – exposure to loss, fragmentation and gain of climate space – is matched to specific response-mediating traits that potentially render species vulnerable, according to expectations from theory and empirical evidence (Fig. 1). Areas of spatial overlap between threats or opportunities and associated vulnerability are then identified. These are areas where traits can potentially exacerbate projected losses and increased fragmentation of climatically suitable areas, or restrain projected gains of newly suitable areas.

We test the practicality of the framework on wide-ranging sub-Saharan African amphibians, using available bioclimatic envelope model and trait data. Our application of the framework reflects situations where only proxies for traits are available and where bioclimatic envelope model projections are available only for wide-ranging species, in our case leading to the exclusion of most narrow-ranging endemics typical of biodiverse montane regions. Worldwide, amphibian populations are declining due to a multitude of threats that include habitat destruction, climate change and the pathogenical fungal disease chytridiomycosis (Blaustein & Kiesecker, 2002; Hof *et al.*, 2011; Li *et al.*, 2013). Climate change, often in tandem with land-use change, is expected to affect large areas of tropical Africa in the future (Hof *et al.*, 2011;

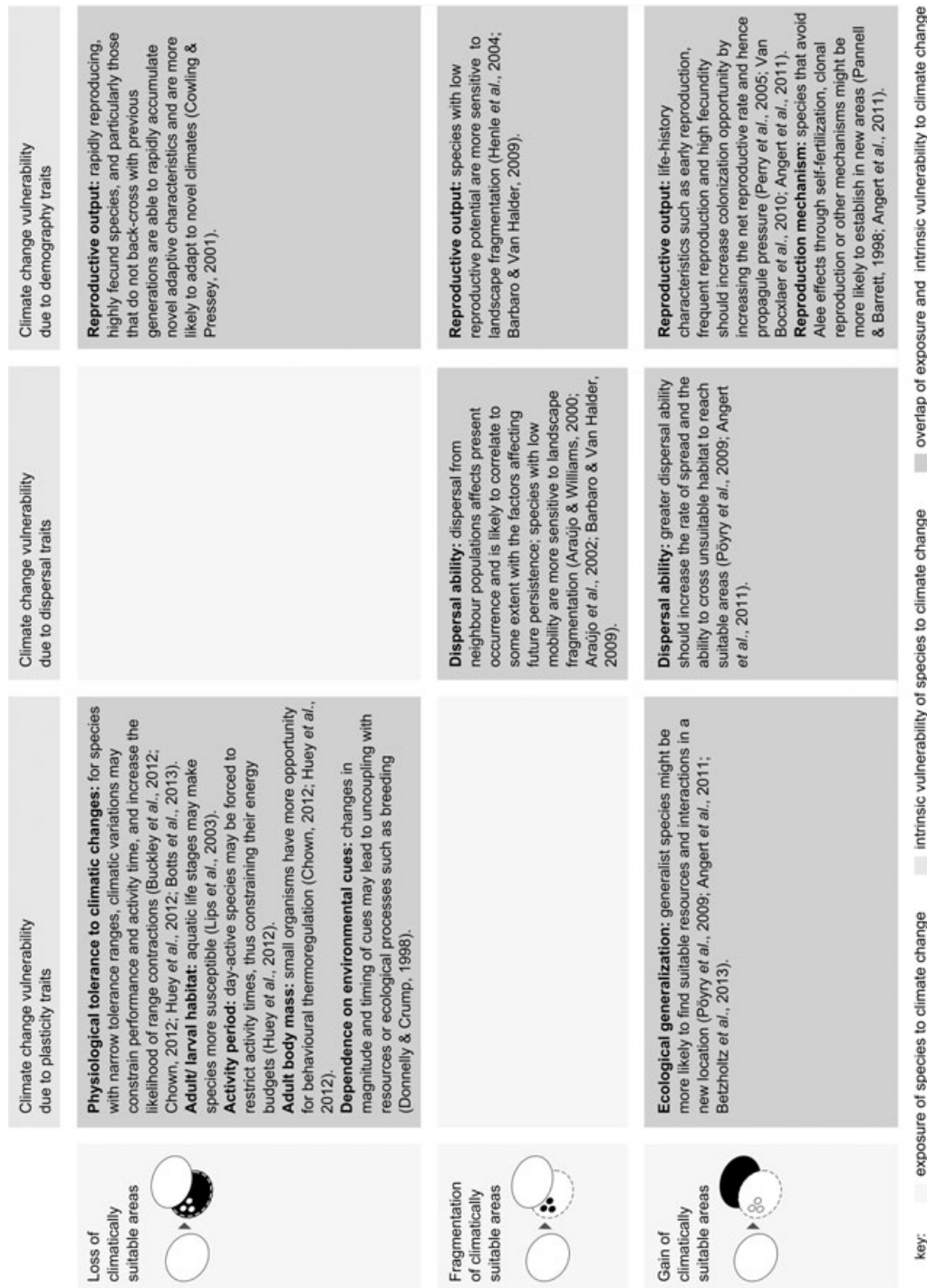


Figure 1 Examples of traits that potentially mediate species' responses to climate change-induced threats and opportunities. Exposure to loss, increased fragmentation and gain of climatically suitable areas are each illustrated with diagrams of the shift from baseline climate space (left) to future climate space (right, closed lines, with the baseline climate space represented by dashed lines, and the component of exposure under consideration highlighted in black). For each of these threats or opportunities, examples are given of potential response-mediating traits associated with species' plasticity, dispersal ability and/or demography, where supported by theoretical and empirical studies across taxa.

Foden *et al.*, 2013). While our aim here is to present a spatially explicit framework for linking threats or opportunities and vulnerability in climate-change risk assessments, the practical application we show can also contribute to a better understanding of climate change risks facing wide-ranging sub-Saharan African amphibians.

MATERIALS AND METHODS

Study species

Our study sample consists of 195 amphibian species (see Appendix S1 in Supporting Information) restricted in their distributions to sub-Saharan Africa, and with available projections of species bioclimatic envelope models (Garcia *et al.*, 2012) and trait data (Foden *et al.*, 2008, 2013). From all 695 species in the original species distribution (Hansen *et al.*, 2007) and trait (Foden *et al.*, 2008, 2013) databases, only 272 had model projections available (excluded were 423 species with fewer than 15 gridded occurrence records), and, of these, 195 also had data for all traits (excluded were 77 species with some trait data missing). Our sample is, therefore, restricted to the widest-ranging species in the dataset, and may not be representative of the overall taxonomic and geographical amphibian diversity patterns in Africa (Appendix S2a–c). In particular, our data exclude most species endemic to biodiverse montane areas such as the Cameroon/ Nigerian highlands and the Eastern Afromontane biodiversity hotspot, and most species in the highest threat categories of the IUCN Red List (Appendix S2d).

Extrinsic threats and opportunities from climate change

We used published baseline (1961–90) and mid-century (2041–60) projections of climatically suitable areas for our 195 amphibians species, at one degree latitudinal–longitudinal resolution (*c.* 111 km × 111 km at the equator), according to mean temperatures of warmest and coldest month and annual precipitation (for detailed methods see Garcia *et al.*, 2012). Future projections were for a multi-model climate ensemble under the A1B greenhouse gas emissions scenario (Nakićenović & Swart, 2000). We used consensus projections obtained by computing the median among seven bioclimatic envelope modelling techniques, in presence–absence format, and assuming unlimited dispersal in future projections. Here, to characterize climate change-induced threats and opportunities, we computed four types of projected changes in climatic suitability: local loss, fragmentation and gain of climatic suitability, and distance to new areas gained. Each metric was quantified per pixel, as described below, yielding maps of changes for each species. Composite maps for our species sample were also obtained by summing the number of species with projected local loss, increased fragmentation, or gain of suitable climate in each pixel.

First, for each species we considered local losses in pixels projected to be climatically suitable in the baseline period but unsuitable in the future. Second, for fragmentation we used a distance-based measure of contagion of suitable climate space. Contagion was measured as the weighted average of the number of suitable pixels among a set of k_i neighbours of a central pixel y_i , where the weight given to the grid cell y_j is $w_{ij} = 1/d_{ij}$, and d_{ij} is the great-circle distance between grid cells y_i and y_j (Araújo *et al.*, 2002; equation 1). Owing to poor dispersal ability of most amphibians, we considered only the first-order neighbours (maximum = 8) adjacent to the central pixel. Changes in contagion were given by the difference between future and baseline contagion, with negative values indicating reduced contagion, i.e. increased fragmentation.

$$c_i = \frac{\sum_{j=1}^{k_i} w_{ij} y_j}{\sum_{j=1}^{k_i} w_{ij}} \quad (1)$$

Third, local gains corresponded to pixels projected to be climatically unsuitable in the baseline period but suitable in the future. Fourth, for species projected to gain newly suitable areas in mid-century, we also computed, for each pixel of newly suitable climate, the great-circle distance to the nearest pixel of baseline suitable climate.

Intrinsic vulnerability to climate change

We sourced the trait data from the IUCN's trait-based climate change vulnerability assessment for amphibians (Foden *et al.*, 2008, 2013). These data are mainly ecological characteristics of species or their ranges rather than traits in a strict sense (*sensu* Violle *et al.*, 2007). From the data available, we selected characteristics that are likely to summarize response-mediating traits under climate change (Fig. 1), and that are not strongly correlated. We thus selected tolerance to temperature and precipitation change, dependence on precipitation cues, dispersal ability and reproductive output (Table 1; see Foden *et al.*, 2008, 2013, for details). For each of these characteristics, we used the climate change vulnerability classification of species by Foden *et al.* (2008, 2013): species were assigned 'high', 'lower' or 'unknown' scores of vulnerability based on the ranking of all sub-Saharan African species in the IUCN database or on pre-defined criteria (see Table 1).

Spatial overlap between threats or opportunities and vulnerability

We spatially assessed where climate-induced threats or opportunities, defined with the metrics of species' exposure to climate change, overlapped with high climate change vulnerability of species according to our selected traits. Following expected interactions between traits and exposure (Fig. 1), we matched plasticity characteristics to local losses, dispersal characteristics to increased fragmentation, and both

Table 1 Species traits used as estimates of intrinsic vulnerability to climate change exposure for sub-Saharan African amphibians. Three climate change-induced threats and opportunities for species were defined based on bioclimatic envelope model projections (Garcia *et al.*, 2012): loss, increased fragmentation, and gain of suitable climate space. For each, different sets of species traits or characteristics of species and their ranges (Foden *et al.*, 2008, 2013) were selected that are likely to mediate species' responses (see Fig. 1).

Extrinsic threats and opportunities from climate change	Intrinsic vulnerability to climate change
Loss	<p>Plasticity</p> <p>Tolerance to temperature change: average absolute deviation for all cells in species' refined range for the monthly means; high risk if ≤ 1.06 °C, i.e. 25% of all 704 sub-Saharan African species in the IUCN dataset with the narrowest tolerance ranges.</p> <p>Tolerance to precipitation change: average absolute deviation for all cells in species' refined range for the monthly means; high risk if ≤ 46.89 mm, i.e. 25% of all 704 sub-Saharan African species in the IUCN dataset with the narrowest tolerance ranges.</p> <p>Dependence on environmental cues: high risk if dependent on rainfall or increased water availability for mass breeding (excludes species buffered by occurring in forests).</p>
Fragmentation	<p>Dispersal</p> <p>Dispersal ability: high risk if not known to have become established outside their natural ranges, not associated with flowing water, and have small ranges (≤ 4000 km², i.e. 25% of all 704 sub-Saharan African species in the IUCN dataset with the smallest ranges).</p>
Gain	<p>Dispersal</p> <p>Dispersal ability: high risk if not known to have become established outside their natural ranges, not associated with flowing water, and have small ranges (≤ 4000 km², i.e. 25% of all 704 sub-Saharan African species in the IUCN dataset with the smallest ranges).</p> <p>Demography</p> <p>Reproductive output: high risk if ≤ 50 offspring annually (where known) or viviparous.</p>

dispersal and demography characteristics to gains (see Table 1). For climatic tolerance, we considered for each species either the tolerance to temperature or to precipitation depending on the variable of highest importance in the bioclimatic envelope models (assessed with permutations within the BIOMOD computing platform in R; Thuiller *et al.*, 2009). We thus identified where projected losses were for species with high vulnerability according to plasticity traits, where projected fragmentation was for species with high vulnerability according to dispersal traits, and where projected gains were for species with high vulnerability according to dispersal or demography traits.

The assessment of spatial overlap was first conducted for all species in our sample, and then individually for groups of species projected to experience different combinations of threats and opportunities. To identify these groups, we ranked species according to each species' overall projected losses, gains and distance to gains of suitable climate. For each species, the overall local losses of climatic suitability L were quantified using the proportion of baseline area of suitable climate (a_i) projected to be lost in the future (l_i ; equation 2). The overall opportunity for gains G was measured as the proportion of baseline area of suitable climate (a_i) projected to be gained in the future (g_i ; equation 3). The surface area across the A pixels of the study area was measured taking into account the curvature of the Earth. The overall distance to new areas D for each species was the mean of the minimum great-circle distances d_{ib} between each pixel gained i and the baseline suitable areas b computed across the N pixels gained (equation 4).

$$L = \frac{\sum_{i=1}^A l_i * a_i}{\sum_{i=1}^A a_i} * 100 \quad (2)$$

$$G = \frac{\sum_{i=1}^A g_i * a_i}{\sum_{i=1}^A a_i} * 100 \quad (3)$$

$$D = \frac{1}{N} \sum_{i=1}^N \min_{vb}(d_{ib}) \quad (4)$$

For each of the metrics considered, we retained the 25% of species with the smallest change values, and the 25% of species with the largest change values. We grouped these species depending on the combination of change level thus defined for the three metrics, with the intention of highlighting the extremes of the distribution of changes. 'Contracting *in situ*' species were projected to suffer the largest losses of baseline climatic suitability, while having little opportunity to move to new suitable areas; 'obligate shifting' species also faced large *in situ* losses but gained suitability in new, distant areas; and 'expanding' species were projected to retain most of their baseline suitability and have large and distant gains outside their distributions.

RESULTS

Our results concern 195 sub-Saharan African amphibians with wider ranges, significantly larger temperature tolerances (P -value < 0.05 , Student's t -test), and a larger proportion of species with higher reproductive output than the remaining

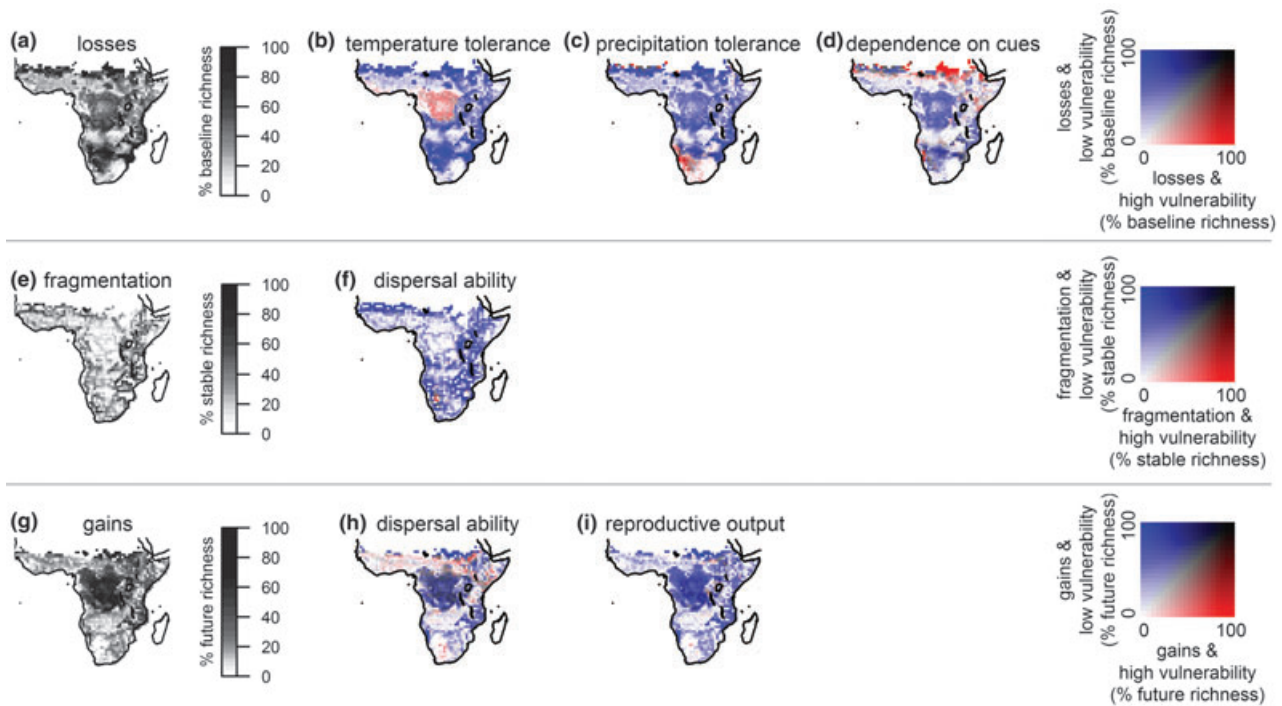


Figure 2 Overlap of climate change exposure and intrinsic vulnerability for a subset of 195 wide-ranging sub-Saharan African amphibians. The greyscale maps show pixel-based proportions of species exposed to losses, increased fragmentation, or gains of climate space: i.e. the proportions of species with baseline climatic suitability in a pixel that lose suitability in that pixel in the future (a), the proportions of species with suitability through time in a pixel that suffer increased fragmentation of climate space around that pixel (e), and the proportions of species with future suitability in a pixel that had no suitability in that pixel in the baseline (g), respectively. The red and blue scale maps compare, for each pixel, the proportions of losses (b–d), increased fragmentation (f) or gains (h–i) that correspond to species with higher vulnerability versus species with lower vulnerability due to selected traits (see Table 1). Different shades on the maps thus indicate dominance of losses, fragmentation or gains for species highly vulnerable (red), species less vulnerable (blue), both species with high and lower vulnerability (black) or none (white). Maps were drawn using quantile classification.

500 species in the dataset (Appendix S2c,e). For this subset, the spatial patterns of climate change exposure (greyscale maps in Fig. 2) showed widespread local losses of climatically suitable space, but a concentration of increased fragmentation in montane areas and local gains in the Congo Basin. Species were also not randomly distributed across sub-Saharan Africa with regard to climate change vulnerability due to selected traits or ecological characteristics of species ranges (Appendix S3a), leading to generally well-defined spatial patterns of overlap between exposure and vulnerability (red and blue scale maps in Fig. 2).

Local losses of climatic suitability were projected throughout most of the study area, with the Congo Basin and the species-poor arid areas of the Sahel and Namibia/Botswana showing the highest proportions of species losing local suitability in the future (Fig. 2a). Geographical areas with greatest proportions of losses overlapping with vulnerability due to traits varied across the three selected traits: the Congo Basin and coastal West Africa for temperature tolerance (red shaded areas in Fig. 2b), South Africa and especially Namibia for precipitation tolerance (red shaded areas in Fig. 2c), and few scattered areas in the Sahel, the Albertine Rift and Namibia for dependence on precipitation cues (red shaded areas

in Fig. 2d). Most projected increases in fragmentation of climate space (Fig. 2e) were for species with low vulnerability due to dispersal traits (blue shaded areas in Fig. 2f). Projected gains (Fig. 2g) may have been overestimated due to poor dispersal ability in the Congo Basin, and especially in areas extending from West Africa to the Ethiopian highlands as well as western South Africa (grey and red shaded areas in Fig. 2h). Gains for species with lower reproductive output were fewer and more scattered throughout the same areas (red shaded areas in Fig. 2i).

Among the three groups of species with different combinations of threats and opportunities, ‘contracting *in situ*’ and ‘obligate shifting’ species had significantly smaller geographical range sizes than ‘expanding’ species or those species not in the three groups (P -value < 0.05, Student’s t -test; see Appendix S3b). For each group, we compared their modelled future distributions of climatic suitability to future projections modified in the following way: losses for species with lower vulnerability due to climatic tolerance were converted into presences, and gains for species with high vulnerability due to dispersal ability were transformed in absences (Fig. 3).

‘Contracting *in situ*’ wide-ranging species occurred mainly in montane areas, which also hold the majority of the

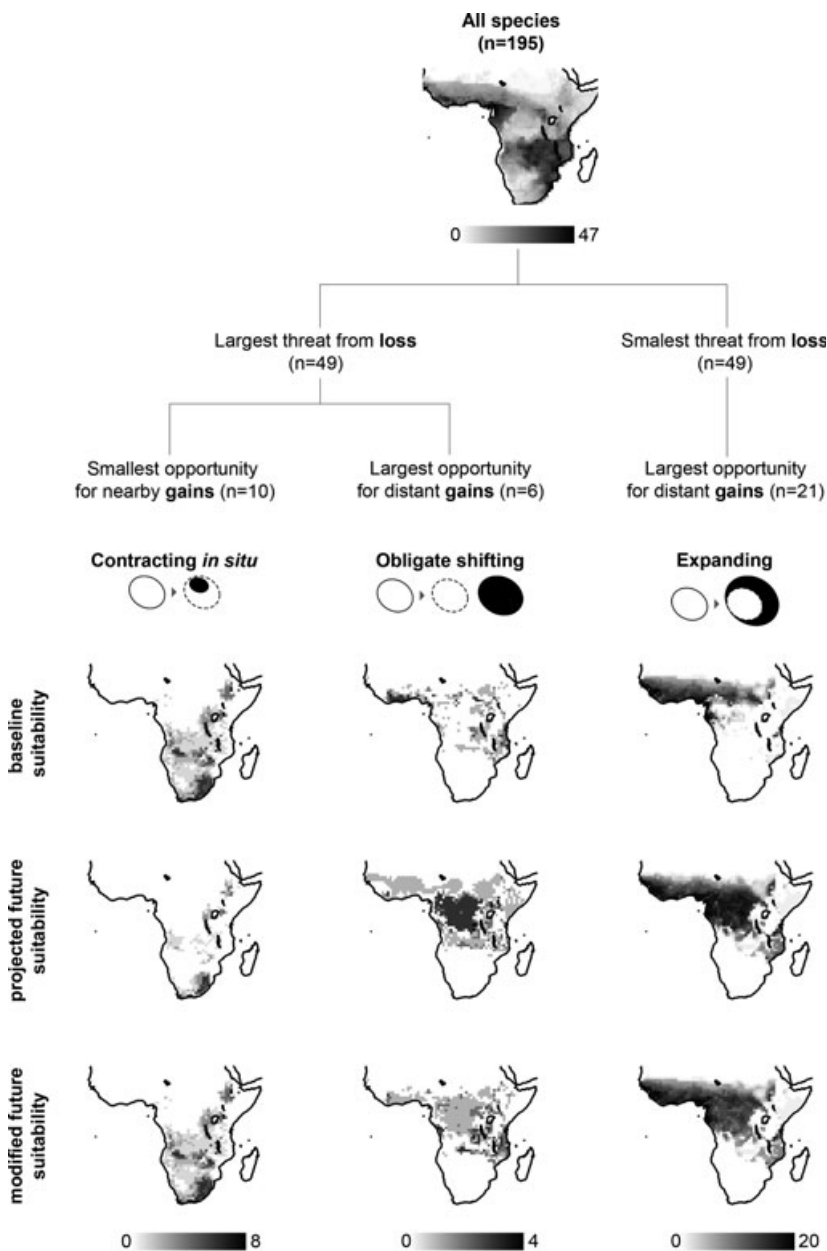


Figure 3 Potential effect of species' climate change vulnerability on projections of climate change exposure for three groups of wide-ranging sub-Saharan African amphibians. Species were classified into 'contracting *in situ*' ($n = 10$), 'obligate shifting' ($n = 6$) and 'expanding' ($n = 21$) based on projected threats and opportunities from climate change. The first node of the tree classifies species based on overall losses of suitable climate, and the second node is based on overall gains of climatic suitability and distances to newly suitable areas. For each metric, only the extreme cases are considered, i.e. species below the 25th and above the 75th percentiles of the distribution of values for all species. The three groups thus obtained are illustrated with diagrams of the shift from baseline climate space (left, white circles) to future climate space (right, dark circles, with the baseline climate space represented by white circles with dashed lines). For each group, the maps show the projected suitability in the baseline (first row) and future (second row) time periods, and the future suitability modified by omitting losses for species with lower vulnerability due to climatic tolerance and the gains for species with poor dispersal ability (third row).

narrow-ranging species excluded from our analysis. Although exposed to large overall losses, species in this group had greater tolerance to climatic variation, and thus the modified future projections were more conservative. For 'obligate shifting' species, occurring in West and East African coastal forests and along the eastern border of the Congo Basin, dispersal traits had the potential to modify projections of exposure. Whereas losses in West Africa were concordant with the species' high vulnerability due to narrow tolerance to climatic variation, gains in the Congo Basin were partly associated with poor dispersers and may thus have been overestimated. Species in the 'expanding' group occurred along a broad band extending from West Africa to west of the Ethiopian highlands. After discounting the few losses of species with lower vulnerability due to the plasticity trait and

the gains of a quarter of species with poor dispersal ability, future projections for this group remained very similar. Overall, correlation between projected and modified future suitability was lowest for 'obligate shifting' species and 'contracting *in situ*' species, and highest for 'expanding' species (Pearson's product-moment correlation coefficient 0.60, 0.74 and 0.97, respectively, P -value < 0.05).

DISCUSSION

Our analysis for wide-ranging sub-Saharan African amphibians shows how a simple framework can be applied that combines familiar projections of climate change exposure with response-mediating traits, to help deliver more realistic climate change risk assessments. The framework teases apart

the threats and opportunities resulting from exposure of species to climate change, and identifies key traits that potentially mediate species' responses to each. Its application is contingent on the availability and quality of both exposure and trait data, as our analysis for sub-Saharan African amphibians clearly illustrates.

Availability of bioclimatic envelope model projections of future climatic suitability is limited by the number of existing records of species occurrence (Feeley & Silman, 2011), and has biased our sample towards wide-ranging species. Trait data availability was a further limitation, although it affected a smaller number of species. Together, these limitations have skewed our sample towards larger geographical range sizes, lower level of current threat, narrower climatic tolerance breadth, and larger reproductive outputs (Appendix S2). Such biases reduce the representativeness of the results and limit the scope for conservation guidance. Indeed, most threatened amphibians were excluded, particularly those from the Cameroon highlands and Eastern Afrotropical centres of diversity. Phylogenetic inference methods exist that could circumvent the bias in the trait data (Nakagawa & Freckleton, 2008; Buckley & Kingsolver, 2012), but, for the bulk of the species excluded here, new approaches that overcome limitations of correlative models are needed to assess exposure of narrow-ranging species to climate change.

Application of our framework is also dependent on the quality of trait data. First, for some of the traits the classification of vulnerability (Foden *et al.*, 2008, 2013) is contingent on the initial pool of species used for scoring (704 sub-Saharan African species). Classes of high and lower vulnerability were defined based on the quantile distribution of trait values across this wider pool of species, yielding a relative classification for all species that is unlikely to reflect the real vulnerability of individual species.

Second, the case of sub-Saharan African amphibians illustrates the framework's application when traits in the strict sense (*sensu* Violle *et al.*, 2007) are largely unavailable, a situation that is common for many taxonomic groups (e.g. González-Suárez *et al.*, 2012). Some of the data used were derived from the characterization of known distributions of species (Foden *et al.*, 2008, 2013) as proxies for traits. One example is tolerance to climatic variation, inferred with statistical approaches relating species ranges to climate variables. Whereas previous studies (e.g. Thuiller *et al.*, 2005a; Feeley *et al.*, 2012) used similar approaches, such proxies do not strictly summarize traits but the interaction between traits and the environment. Climatic tolerance inferred with these approaches may represent under-estimates when climatic niches realized in the present are truncated (Feeley & Silman, 2010). The finding that upper thermal limits tend to be highly conserved while lower limits are highly variable across organisms (Araújo *et al.*, 2013) further indicates that such proxies may be misleading. Only the physiological limits of species could indicate their full capacity to adapt to climatic changes through plastic adaptation. One exemplar study is that of Arribas *et al.* (2012), where an experimental approach

was applied to estimating the safety thermal limits and acclimation capacity of water beetles. Likewise, estimates of species' dispersal abilities derived from empirical data on organism movement (e.g. Gamble *et al.*, 2007), phylogenetic distances (Arribas *et al.*, 2012), or morphological or life-history traits (e.g. Baselga *et al.*, 2012; Whitmee & Orme, 2013) would more reliably predict the ability of species to track suitable climates than estimates based on known geographical ranges of species.

Despite the shortcomings of the trait and exposure data used here, our results illustrate how interpretation of spatial projections of species' exposure to climate change can be altered with consideration of species' climate change vulnerability. Projections under climate change have been shown elsewhere to vary because of assumptions regarding the thermal tolerance of species (Feeley *et al.*, 2012), and differences in dispersal capacity (Urban *et al.*, 2012). Our analysis for wide-ranging sub-Saharan African amphibians highlights the Congo Basin and arid regions of Southern Africa, where projected losses were compounded by species' sensitivity to climatic variation, and expected gains were precluded by poor dispersal ability (Fig. 2). Tropical ectotherms have been highlighted for their vulnerability to climate change because they are living close to their upper thermal limits (Deutsch *et al.*, 2008; Huey *et al.*, 2009) and have narrower thermal breadths (Sunday *et al.*, 2012). The lowland tropics in particular have been suggested to hold a high concentration of ectotherms sharing vulnerability traits (Huey *et al.*, 2012), and to face biotic attrition in the future (Colwell *et al.*, 2008). The shallower temperature gradient in tropical lowlands (Colwell *et al.*, 2008) increases distances required to track suitable climates, potentially imposing a challenge to poor dispersers.

Among the groups of wide-ranging amphibians exposed to different combinations of threats and opportunities, those most exposed – 'contracting *in situ*' and 'obligate shifting' species – showed the strongest modifying effect of vulnerability on projections of exposure (Fig. 3). Whereas poor dispersal ability rendered projected gains to be unlikely for 'obligate shifting' species, losses for 'contracting *in situ*' species were discordant with the group's lower vulnerability with respect to plasticity. Exposure of the narrow-ranging montane species excluded from this study probably mirrors more closely that of our 'contracting *in situ*' group, which includes species with ranges among the smallest of our sample and encompassing mountain regions (Fig. 3). For narrow-ranging species, contraction of the available marginal climatic conditions that are suitable for them may play an important role (Williams *et al.*, 2007; Ohlemüller *et al.*, 2008). At the same time, in the topographically diverse regions where these species occur, microclimates not captured at the coarse scale used here may facilitate adaptation to changing climates (Pearson, 2006). Besides the potential threat from climate change, the high-elevation, range-restricted species with low fecundity that were excluded from our study (Appendix S2) are also susceptible to declines associated with the chytridiomycosis disease (Bielby *et al.*, 2008). By contrast, future

projections for ‘expanding’ species remained largely unchanged after consideration of traits, although this may result from our simplistic approach whereby we retained all gains by good dispersers irrespective of the distances involved. Nevertheless, the current levels of loss and fragmentation of natural ecosystems are likely to pose an important challenge to dispersal (Opdam & Wascher, 2004).

We propose that application of our framework can provide information about the causes, spatial distribution and conservation implications of climate change risk (Thomas *et al.*, 2011). Conservation needs will differ between species projected to partly retain suitability where they occur and those for which suitability shifts to new areas. In the latter case, gains in new areas may compensate losses and even lead to an increased, displaced, climate space. However, if newly suitable areas are distant, poor dispersal ability may place these ‘obligate shifting’ species at risk. In risk assessments based on changes in total area of climatic suitability (e.g. Thuiller *et al.*, 2005b; Araújo *et al.*, 2006; Huntley *et al.*, 2006; Feeley *et al.*, 2012; Triviño *et al.*, 2013) such species may be classified as ‘winners’ and thus be overlooked. Indeed, the ‘obligate shifting’ amphibians in our study were projected to increase their overall climate space, but were flagged for the low *in situ* persistence and the large discontinuity between baseline and future climate space, compounded by poor dispersal ability.

Previous frameworks to guide conservation under climate change separated the threat of loss from opportunities for gains of climate space (Thomas *et al.*, 2011; Arribas *et al.*, 2012). The framework we present here considers an additional extrinsic factor that is seldom explored – changes in the level of fragmentation of climate space (but see Serra-Diaz *et al.*, 2014). Besides influencing the probability and speed of range expansion (Hodgson *et al.*, 2011), the level of aggregation of species records has been found to be a strong covariate of local extinction risk of bird species in Britain (Araújo *et al.*, 2002). At the coarse resolution of our study, our measure of fragmentation and the correspondent trait provide some indication on the risk of isolation from surrounding areas of suitable climate, although with more limitations in topographically diverse regions. The level of fragmentation characterized through the metric of contagion is particularly important at fine scales, where the risk from both increased isolation and decreased area of fragments of suitable climate becomes more evident. Measures of contagion that consider both effects could thus be used at finer scales, borrowing from metapopulation and landscape theory (Hanski, 2005). Yet the parallel between within-generation habitat fragmentation at the landscape level, on one hand, and increased fragmentation of climate space at larger spatial and temporal scales like the ones used here, on the other hand, is not clear-cut and needs more attention.

Our framework relies on the identification and quantification of traits that potentially mediate the effect of climate change exposure on species. Important response-mediating traits are likely to vary across taxa, and further studies of

trait correlates of observed changes in ranges under changing climates can help expand and adapt our list of examples (Fig. 1). Where available, more precise and reliable estimates of response-mediating traits allow for a closer coupling of bioclimatic envelope models with traits, leading to projections that are more appropriate for conservation planning. For example, measures of dispersal capacity can be used to filter, pixel by pixel, projected gains of climate space depending on their distance from present distributions (see Bateman *et al.*, 2013, for a review of options of dispersal scenarios in predictive modelling). Similarly, physiological climatic limits can provide the bounds for species persistence in modelling exercises (Arribas *et al.*, 2012; Summers *et al.*, 2012). Projections of climate change exposure typically discount other important factors such as biotic interactions, local population adaptations and landscape structure, but assessing the robustness of projections to the effect of response-mediating traits is one crucial step towards increased realism.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of sub-Saharan African amphibians included in the study.

Appendix S2 Representativeness of the subset of sub-Saharan African amphibians used in the study.

Appendix S3 Comparison of climate change vulnerability traits across different groups of sub-Saharan African amphibians.

BIOSKETCHES

Raquel A. Garcia is interested in the climate change risks facing African biodiversity, and in combining different data and approaches for risk assessments in Africa and elsewhere.

Author contributions: N.D.B., R.A.G., W.B.F., M.C. and M.B.A. discussed the original idea, and R.A.G. and M.C. conceptualized the study. R.A.G. performed the analysis, and R.A.G. wrote the paper with comments from all authors. A.G. and W.B.F. provided trait data.

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